Comparative demography of three coexisting Acer species in gaps and under closed canopy

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Comparative demography of three coexisting *Acer* species in gaps and under closed canopy

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Abstract

Questions: 1. Is there a trade-off between gap dependency and shade tolerance in each of the life-history stages of three closely related, coexisting species, *Acer amoenum* (*Aa*), *A. mono* (*Am*) and *A. rufinerve* (*Ar*)? 2. If not, what differences in life-history traits contribute to the coexistence of these non-pioneer species?

Location: Ogawa Forest Reserve, a remnant (98 ha), species-rich, temperate deciduous forest in central Japan (36°56' N, 140°35' E, 600 - 660 m a.s.l.).

Methods: We estimated the demographic parameters (survival, growth rate and fecundity) by stage of each species growing in gaps and under closed canopy through observations of a 6-ha permanent plot over 12 years. Population dynamics were analysed with stage-based matrix models including gap dynamics.

Results: All of the species showed high seedling and sapling survival rates under closed canopies. However, demographic parameters for each growth stage in gaps and under closed canopies revealed inter-specific differences and ontogenetic shifts. The trade-off between survival in the shade and growth in gaps was detected only at the small sapling stage (height < 30 cm), and *Ar* had the highest growth rate both in the shade and in the gaps at most life stages.

Conclusions: Inter-specific differences and ontogenetic shifts in light requirements with life-form differences may contribute to the coexistence of the *Acer* species in old-growth forests, with *Aa* considered a long-lived sub-canopy tree, *Am* a long-lived canopy tree, and *Ar* a short-lived, 'gap-phase' sub-canopy tree.

Keywords: Demography; Growth rate; Ogawa Reserve; Shade tolerance; Survival; Trade-off; Transition matrix model.

Nomenclature: Satake et al. (1989).

Abbreviations: *Aa* = *Acer amoenum*; Adt1/Adt2 = Adult stages 1 & 2; *Am* = *A. mono*; *Ar* = *A. rufinerve*; Fadt1/2 = Female stages 1, 2; Juv1/2 = Juvenile stages 1, 2; Madt1/2 = Male stages 1, 2; Sapl = Large sapling; Saps = Small sapling; Sdl = Seedling.

Introduction

The dichotomy between gap dependent (i.e. light-demanding) species and shade-tolerant species is a well accepted paradigm in studies of tree life history variation within mixed forests (Swaine & Whitmore 1988; Denslow 1987). A trade-off between the capacity for rapid growth in large gaps and the ability to survive in the shaded understorey is assumed to be one of the underlying determinants of this dichotomy and a key factor in coexistence in a forest community (Denslow 1987; Welden et al. 1991; Kitajima 1994; Pacala et al. 1996). Recent studies have recognized that these varying life-history traits have a continuous, rather than discrete, distribution and that many species' traits are intermediate between the two extremes (Clark & Clark 1992; Dalling et al. 2001; Wright 2002; Wright et al. 2003). However, life-history differences among non-pioneer species are not well understood across developmental stages. Also, the ubiquity of the dichotomy paradigm has not been widely tested within a set of species that lack extreme ecological characteristics (but see Clark & Clark 1992).

Trees have long life spans and experience highly variable light conditions over their life time with dramatic changes in growth form from seedlings to adults. Clark & Clark (1992) found evidence for size-dependent or ontogenetic changes in growth and survival of tree species in a tropical rain forest. Dalling et al. (2001) found that *Alseis blackiana* (a tropical canopy tree species) exhibited ontogenetic shifts of life-history traits: it requires canopy gaps with high light levels for germination, but is shade tolerant at the seedling and sapling stages. In contrast, Lei & Lechovicz (1990) suggested that the shade-tolerance of juvenile *Acer saccharum* is constrained functionally by requirements set by the canopy environment that adults

will occupy, rather than by an ontogenetic shift. Regardless of these differences in viewpoint, it is important to understand the characteristics of all life-history stages of tree species in order to elucidate ecological mechanisms that govern species assemblage organization (Clark & Clark 1992).

The genus *Acer* (maple) is one of the most diverse taxonomic groups of trees in the northern hemisphere (Van Gelderen et al. 1994). Among the species, there is considerable diversity in life history traits and tree architecture; there are differences both between understorey and canopy species, and between early and late successional species (Ackerly & Donoghue 1998). While comparative studies of maples have demonstrated significant inter-specific variation in life history, morphology and physiology in relation to forest light environments (Sakai 1987, 1990; Lei & Lechowicz 1990, 1997; Sipe & Bazzaz 1994, 1995, 2001; Peters et al. 1995; Tanaka 1995), they have focused on the juvenile stages only. There are no comparative studies of coexisting *Acer* species that span the entire life history. Responses to the different light conditions at different life stages may play a major role in tree species coexistence in forests, so understanding forest species diversity will require comprehensive approaches to comparative population dynamics.

Here, we examine the differences in demographic parameters among three coexisting *Acer* species in a temperate forest community using data collected over 12 years spanning all of the life-history stages. We evaluate the demographic parameters derived from trees growing in the shade and in gaps to answer the following questions: 1. Is there a trade-off between gap dependency and shade tolerance in each of the life-history stages of these non-pioneer species? 2. If not, which intra-generic differences in life-history traits contribute importantly to the coexistence of these *Acer* species?

Material and Methods

Study site and species

The Ogawa Forest Reserve is a remnant (98 ha), species-rich temperate deciduous forest in central Japan (36°56' N, 140°35' E, 600 - 660 m a.s.l.). The mean annual temperature and precipitation (from the nearest three weather stations of the Meteorological Agency, all within 30 km) were 9.0 °C and ca. 1750 mm, respectively.

The total basal area and the density of trees ≥ 5 cm in DBH in 1989 were 32.3 $m^2.ha^{-1}$ and 841 stems /ha. The dominant tree species in terms of basal area were *Quercus serrata* (26.6% of the total basal area), *Fagus japonica* (19.8%) and *F. crenata* (8.5%). Dwarf bamboo (*Sasa* and *Sasaella* spp.) covered some of the forest floor. Disturbances related to human activities, including grazing and fire affected the forest until the 1930s, especially at its margins (Tanaka & Nakashizuka 1997). Tree fall gaps caused by strong winds, particularly those associated with autumn typhoons and very low pressure weather systems in late winter have been the most dominant agents of disturbance since the 1930s (Abe et al. 1995, Nakashizuka 2002). Masaki et al. (1992) and Nakashizuka et al. (1992) give a more detailed description of the composition and dynamics of this forest.

The three species selected for the study, *Acer amoenum* (*Aa*), *A. mono* (*Am*) and *A. rufinerve* (*Ar*), commonly occur in temperate deciduous forests of Japan. In the forest reserve, *Aa* is the most dominant of the three species (ranked 8th in total basal area among the 55 tree species), followed by *Am* and then *Ar*. A total of 12 *Acer* species exist in this forest, among which *Aa*, *Am* and *Ar* were the most abundant.

Two varieties of *Acer mono* (Satake et al. 1989) occur here: *A. mono* var. *marmoratum dissectum* and *A. mono* var. *ambiguum*. Within the reserve, ca. 90% of *A. mono* individuals with DBH ≥ 5 cm are *A. mono*. var. *marmoratum dissectum*. In this study we did not distinguish between varieties. To clarify any subtle ecological differences between the types is a challenge for the future.

We divided the life histories into five major growth stages based on size observed in the field: 1. Current year seedling (Csdl); 2. Seedling (Sdl, height < 30 cm); 3. Small sapling (Saps, 30 cm ≤ height < 2 m); 4. Large sapling (Sapl, height ≥ 2 m, DBH < 5 cm); 5. Tree (DBH ≥ 5 cm) (see Tanaka & Nakashizuka 2002). The tree stage was further subdivided according to the reproductive habit of the respective species. In *Aa* and AM, the tree stage was subdivided into two juvenile and two adult stages at the critical size of reproduction (see Field methods). The subdivisions for *Aa* were Juv1 (DBH 5-10 cm); Juv2 (DBH 10-15 cm); Adt1 (DBH 15-25 cm); Adt2 (DBH ≥ 25 cm). For *Am*, the subdivisions were Juv1 (DBH 5-10 cm); Juv2 (DBH 10-20cm); Adt1 (DBH 20-40 cm); Adt2 (DBH ≥ 40 cm). Subdivisions of the adult stages for *Aa* and *Am* were made at around the mid-value between the lower boundary of adult stage and maximum DBH. In *Ar*, since all the individuals with a DBH ≥ 5 cm flowered and were dioecious (changing sex from male to female; cf. Matsui 1995; Nanami et al. 2004; H. Tanaka unpubl. data), the tree stage was subdivided into two male stages (Madt1, DBH 5-20 cm; Madt2, DBH ≥ 20 cm) and two female stages (Fadt1, DBH 5-20 cm; Fadt2, DBH ≥ 20 cm).

Field methods

In the central part of the reserve, a 6-ha (200 m × 300 m) permanent plot was established in April 1987. Different sampling methods were applied in this plot to estimate demographic parameters of the three *Acer* species at different developmental stages. All the trees (DBH ≥ 5 cm) in the 6-ha plot were identified, tagged and mapped. DBH of the trees was measured every two years until 1993 and every four years thereafter for the newly recruited stems. The status of tree crowns (canopy, suppressed, in gap) was also recorded at each census. Saplings were identified and tagged in 651 quadrats (2 m × 2 m) located at every intersection of a 10 m × 10 m grid overlaying the 6-ha plot. Sapling height and DBH (for saplings ≥ 2 m height) were also recorded every two years.

To assess seed and seedling demography in a 1.2-ha area within the 6 ha plot, we established 263 seed traps (0.5 m^2) and an adjacent 1 m × 1 m quadrat. The trap-quadrat combinations were arranged regularly in a matrix at a distance of 7.1 m from one another. Since there were no *Ar* female trees in the 1.2-ha sub-plot, an additional 48 combinations of the seed trap and seedling quadrat (same design) were established in a 0.15-ha area with two reproductive trees. Seeds that fell into the seed traps were collected every two weeks during the season of seed formation and seed fall, and every four weeks over the rest of the growing season. Collected seeds were identified to species, counted and classified according to their appearance and content (sound, empty, immature, damaged by insects or other animals). Current year seedlings in the seedling quadrats were identified, marked and recorded every two weeks April through August, and every four weeks September through December. Seedlings in the quadrats that were older than one year at the outset were identified and marked, and their heights were measured annually; surviving new seedlings were treated similarly. Details of these field procedures are provided by Shibata & Nakashizuka (1995) and Tanaka (1995).

Canopy gap creation by single or multiple tree falls is the major disturbance mode in this forest (Nakashizuka et al. 1992; Tanaka & Nakashizuka 1997). Canopy gaps, defined as areas with a canopy less than 10 m above the ground, were recorded every two years (from 1987) in the 6 ha plot using canopy censuses of 2400 5 m × 5 m sub-quadrats.

To examine the demography of seed and seedlings in gaps, additional censuses were conducted in four newly created gaps (created in 1988, 1989, 1989 and 1990) in the forest using a method similar to that used in the 1.2-ha sub-plot. In total, 45 extra sets of seed traps (0.5 m^2) and 1 m × 1 m seedling quadrats were established in the new gaps. Seed fall and the emergence and survival of seedlings were monitored as for the 1.2-ha sub-plot.

For additional censuses of saplings in gaps, we established 115 quadrats (5 m × 5 m) in 1990 and 1992 in 55 canopy gaps in the forest. Saplings in the gaps were assessed every two years until 1996 with the census methods used in the 2 m × 2 m sapling quadrats (Abe et al. 1995).

To estimate the reproductive status of the three *Acer* species through time, we recorded flowering and fruiting habits every year from 1990 to 1995 for ca. 30 individuals per species of various sizes and canopy conditions. We subjectively categorized the flowering condition of each sample tree into five levels (0 = none to 4 = very abundant) and derived the flowering index for each tree as a mean of the scores for the six years. For *Ar*, we made a census of flowering and fruiting of all trees and most of the large saplings in the 6 ha plot. Since flowering individuals of *Ar* constantly bore abundant flowers, we only checked either flowering or non-flowering for *Ar*. We applied a modified form of a logistic regression equation (Thomas 1996) and estimated the critical size of reproduction by calculating the inflection point of the curve. We defined the boundary between reproductive (adult) and non-reproductive (juvenile) individuals in the matrix models using these data.

Analyses of survival and growth rate

In addition to the transition matrix analyses (see below), we compared the survival and relative growth rates (RGR) of the three species at each life stage under closed canopy and in gaps. Since we could not sample destructively, RGR was calculated as RGR of height for Sdl and Saps, and RGR of DBH for the larger life stages. All the statistical analyses were performed with JMP 5.0.1J (Anon. 2001).

Matrix model

Transition matrix models project the dynamics of populations by matrix algebra. The population transition matrix **A** is composed of elements a_{ij} that describe transition probabilities among the life stages from stage *j* to *i* during a time interval from year *t* to year *t*+1. The maximum likelihood estimate of the probability of transition from stage *j* to stage *i* is given by the proportion of individuals in stage *j* in year *t* that appeared in stage *i* in year *t*+1. Elements along the diagonal represent the probabilities of staying at the same stage (stasis), elements below the diagonal represent the probabilities of growth to larger stages (progression) and elements above the diagonal represent the probabilities of downgrading to smaller stages (retrogression, Silvertown et al. 1993). Elements at the transitions from the reproductive stages to the first stages represent the fecundity (*per capita*

reproduction). Describing the stage distribution of the population as a column vector $\boldsymbol{n}$, the distribution after one time interval will be given as: $n_{t+1} = \mathbf{A}\boldsymbol{n}_t$. The column vector will converge after intervals as: $\boldsymbol{n}_{t+1} = \lambda \boldsymbol{n}_t$, where the asymptotic λ is the population growth rate in equilibrium and is given by the dominant eigenvalue of the matrix **A** (Caswell 2000).

We applied the parametric bootstrap (Efron & Tibshirani 1993) to associate a confidence interval (CI) with the estimated population growth rate λ for each species according to the method of Caswell & Kaye (2001). We generated bootstrap estimates of fecundity for stage *j* as the mean of *Nj* Poisson random variates, with the mean equal to the observed mean fecundity. A bootstrap estimate of column j of the rest of the matrix was obtained by drawing a sample of size *Nj* from a multinomial distribution equal to the observed transition probabilities. We took 2000 bootstrap sample matrices, yielding 2000 bootstrap estimates of the population growth rate λ. We calculated 95% Confidence interval for λ as the 2.5th and 97.5th percentiles of this bootstrap distribution.

The stable size distribution *n* and the reproductive values of the stages are given by the right eigenvector and the left eigenvector of **A**, respectively.

The sensitivity of the population growth to a small change in each transition (i.e. $\partial\lambda / \partial a_{ij}$) is calculated by the product of the *j*-th element of stable size distribution vector (*n*) and the *i*-th element of the reproductive values vector (Caswell 2000). To compare or estimate the contribution of each transition to the population growth rate, differences in measuring the scales of the transitions should be considered carefully. The elasticity that de Kroon et al. (1986) introduced is a method to treat the contribution proportionally, and is defined as: $e_{ij} = (a_{ij} / \lambda) * (\partial\lambda / \partial a_{ij})$. We used the elasticity e_{ij} to estimate the proportional contributions of each stage to the population growth of each species.

The whole life cycle of each species (except for the seed) was divided into eight stages as described in Study site and species. From the demographic data for eight years, from 1987 to 1996, we constructed three types of matrix models for each species:

1. Shaded population model: All of the transition probabilities were calculated only for the individuals under a closed canopy. In this case, we presume that the populations of each species are under a closed canopy and are shaded throughout their life cycle. The survival, growth, and mortality of seedlings and saplings in the shaded conditions were based on the shaded quadrats.

2. Gap population model: All of the transition probabilities were calculated only for the individuals in gaps. The populations of the three maples were assumed to be in a gap environment through the entire life cycle. All adult trees that reached the canopy layer were included in the gap population.

3) Combined population model: The model consisted of shaded and gap sub-populations (Fig. 1). In this model, the sub-populations change their canopy conditions according to the transition probability of canopy conditions (i.e. transition probability between closed canopy and gaps). The annual transition probability of canopy condition in this forest was calculated by Nakashizuka et al. (1992): gaps accounted for 6.2% of the whole canopy area in the plot and 0.42% of the whole canopy area become gaps annually. Assuming that the proportion of gap areas and gap formation rate are stable, we calculated that the annual transition probability of the closed canopy area to gaps to be 0.45%, and that the probability of gap areas returning to closed canopy was 6.8%. In constructing the combined population model, we simply assumed that the proportion of gap areas is common to the individuals of all life stages, although gap architecture (Hubbel & Foster 1986; Tanaka & Nakashizuka 1997) could have some influence on the response of individuals of different size classes (Abe et al. 1998).

We constructed all the matrices as a weighted mean of the matrices of different observation years. This construction is equivalent to pooling the transition data on all individuals in each stage and calculating the maximum likelihood estimates of the matrix from the pooled data (cf. Caswell and Kaye 2001). While the transition probabilities per year for the two smallest life stages (Csdl and Sdl) were calculated directly from the observed data, the transition probabilities per year for the larger life

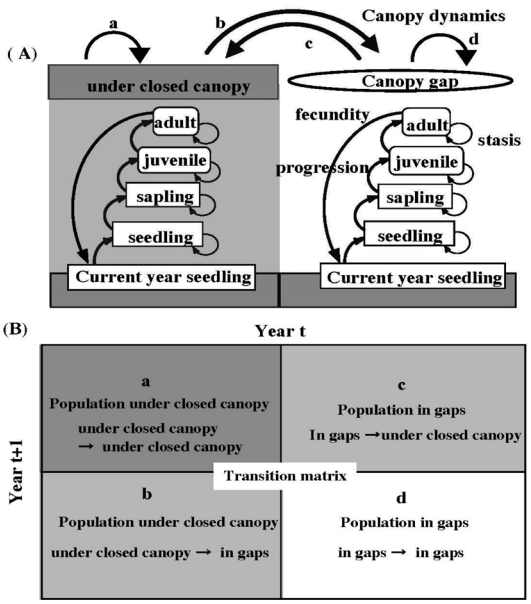

Fig. 1. Scheme of (**A**) Population dynamics under closed canopy and in gaps, and (**B**) transition matrix of the metapopulation incorporating the canopy dynamics. a, b, c and d in (**A**) correspond to the a, b, c, and d in the matrix in (**B**).

stages were calculated from the transition probabilities observed over two years. If no individuals in the largest Adt2 stage died during the eight year study period (as in the the gap population of *Aa* and the shaded and gap populations of *Am*), we calculated a minimum annual mortality rate (*d*) so that the number of individuals that died during the whole study period was < 1, and adopted 1-*d* as the annual survival rate.

While fecundity usually means *per capita* seed production, we defined it here as the mean annual emergence of current year seedlings per adult tree (per capita seedling emergence). Seedling emergence per unit basal area of adult tree was estimated as the emerged seedling density (number of seedlings/m^2/year) divided by the basal area density (basal area/m^2) of the reproducing adult trees in a 1.2 ha sub-plot (0.15 ha sub-plot for *Ar*). *Per capita* seedling emergence for each adult size class was calculated as follows:

(seedling emergence per unit basal area) ×
(basal area calculated from median DBH value of size class).

Standardization by basal area was adopted because reproductive biomass scales linearly with basal area (Niklas 1993; Wright et al. 2003). We used the estimated fecundity (*per capita* seedling emergence) both for gap and shaded populations because of the technical difficulty in estimating the fecundity independently. This might cause over estimation of fecundity for shaded populations, especially for *Am* which seldom reproduces under suppressed conditions.

For the calculation of the matrix model analyses, the computer software, Mathematica Ver. 3.0 (Anon. 1995) and Poptools Ver. 2.7 (http://www.cse.csiro.au/poptools/) were used. For the statistical analyses, Jump 5.0.1J (Anon. 2001) was used.

Results

Population structure at outset

Ar had a size class distribution of trees (i.e. DBH ≥ 5 cm) quite different from those of *Aa* and *Am* (Fig. 2). *Aa* and *Am* had distinct L-shaped size class distributions, whereas *Ar* had a bell-shaped size distribution. *Am* had the largest maximum DBH (80 cm) and many individuals reached the canopy layer. Some individuals of *Aa* also reached the canopy, but most of the trees stayed in the suppressed sub-canopy layer. The maximum DBH of *Ar* was the smallest, but a larger proportion of individuals reached the canopy layer at relatively small DBH sizes.

In contrast to size distribution of trees (DBH ≥ 5 cm), when the population structure was expressed as life stages, including seedling and sapling stages, an L-shaped distribution was found for all three species (Fig. 3). They all showed a large preponderance of seedling and sapling

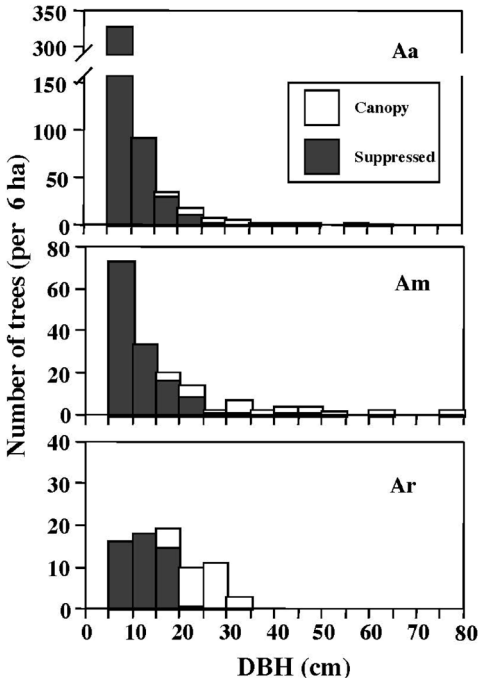

Fig. 2. Population size class structure (individuals with DBH > 5 cm) for three *Acer* species in a 6-ha permanent plot in 1989.

stage individuals (Fig. 3) compared to later life stages. Reflecting the shape of tree (DBH ≥ 5 cm) size class distribution (Fig. 2), the Juv1 stage (5 cm ≤ DBH < 20 cm) of *Ar* occurred at higher density than the Sapl stage (Height ≥ 2 m, DBH < 5 cm).

Survival and growth of seedlings and saplings under closed canopies

All of the species had a relatively high survival rate for current year seedlings under closed canopy (0.23, 0.21,

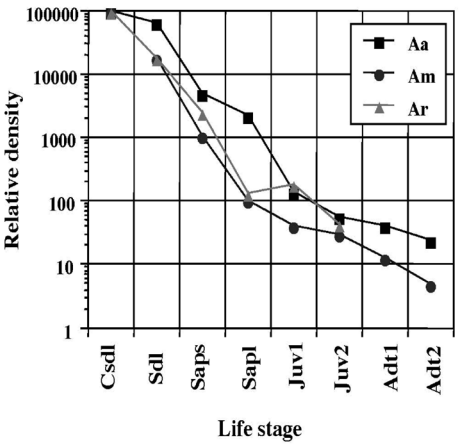

Fig. 3. Population stage class structure in 1989 of three *Acer* species (including all life cycle stages). For *Acer rufinerve*, juvenile1 and juvenile2 stage refer to adult1 and adult2 stages, respectively (the juvenile stage is skipped in this species). Y-axis indicates relative density of individuals (log-scale).

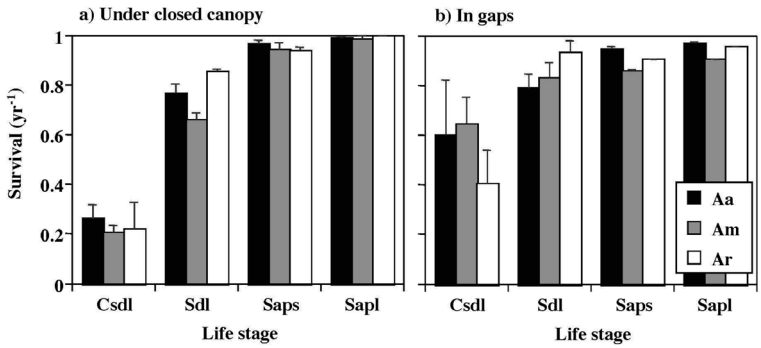

Fig. 4. Survival of current year seedlings, seedlings and saplings (**a**) under closed canopy and (**b**) in gaps. Means + SE. No significant differences were found among the three species at any life stage (Tukey's HSD test, $p > 0.05$).

0.24/year, for *Aa*, *Am* and *Ar*, respectively) in comparison with the other shade-tolerant species in this community (Niiyama & Abe 2003; T. Nakashizuka, et al. unpubl.) and there were no significant differences among the *Acer* species (Fig. 4a, Tukey's HSD test, $p > 0.05$).

Survival rate of the seedlings and saplings under closed canopy increased with progressively higher life stage or increasing size class, and there were no significant differences between species for any size class (Fig. 4a).

In contrast to survival rate, the RGR of height under closed canopy differed marginally or significantly between the species at each life stage (Fig. 5b). Furthermore, the order of RGR among the three species changed with size classes. The Seedling (Sdl, height < 30 cm) and Large sapling (Sapl, height ≥ 2 m, DBH < 5 cm) stages of *Ar* showed marginally faster growth rate for height and significantly faster growth rate for diameter than those of *Aa*. In contrast, Small saplings (Saps, 30 cm ≤ height < 2 m) of *Aa* had a significantly higher RGR than those of *Ar* (Fig. 5a). *Am* and *Ar* had negative mean relative growth rates at the small sapling stage, while *Aa* maintained a positive mean growth rate. *Am* always exhibited a growth rate intermediate between *Aa* and *Ar* (Fig. 5a).

Survival and growth of seedlings and saplings in gaps

Significantly higher survival of current year seedlings in gaps than under a closed canopy was detected for *Am* (Fig. 4, Tukey's HSD test, $p < 0.05$) and marginally detected for *Ar* (Fig. 4, Tukey's HSD test, $p = 0.07$). Survival of seedlings in gaps was not significantly higher than under a closed canopy for any of the three species (Fig. 4, Tukey's HSD test, $p > 0.05$). Survival of current year seedlings and seedlings in gaps was not significantly different between the three species (Fig. 4b, Tukey's HSD test, $p > 0.05$). Survival of saplings was comparable among the species (no statistical tests were performed owing to insufficient replication at census time) and also similar between gaps and under closed canopy (Fig. 4).

The increase in growth rate in response to the improved light conditions in gaps was largest for seedlings and saplings of *Ar*, intermediate for those of *Am* and the smallest for those of *Aa* (Fig. 5). Significantly higher growth rate in gaps than under closed canopy was detected in seedling and sapling stages for *Ar*, but was detected only in the seedling stage for *Aa* and *Am*.

Seedlings and saplings of *Ar* consistently had significantly higher growth rates in canopy gaps than those of *Aa* (Fig. 5a). Under closed canopy and in gaps, *Am* consistently showed a growth rate intermediate between those of *Aa* and *Ar*.

Growth of trees under closed canopy and in gaps

Trees (DBH > 5 cm) of all species growing in gaps (or that reached the canopy layer) exhibited higher growth rates than those of the same size classes under closed

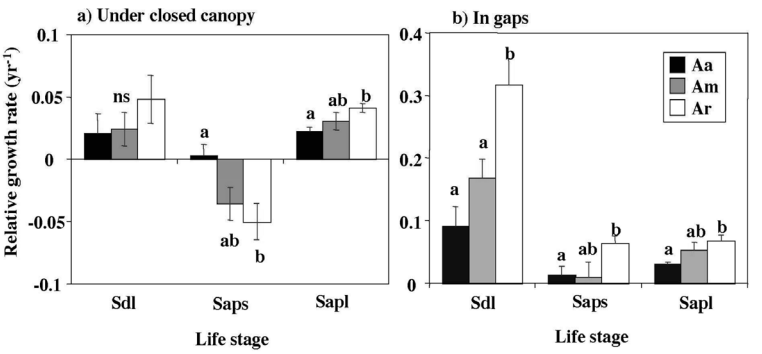

Fig. 5. Relative growth rate (RGR) of seedlings and saplings (**a**) under closed canopy, (**b**) in canopy gaps. Means + SE. Different letters indicate significant differences between the species at each size class (Tukey's HSD test, $p < 0.05$).

Table 1. Transition probability matrices for three *Acer* species, (**a**) under a closed canopy and (**b**) in gaps.

a) Under closed canopy

A. amoenum

	Csdl	Sdl	Saps	Sapl	Juv1	Juv2	Adt1	Adt2
Csdl	0	0	0	0	0	0	140	560
Sdl	0.266	0.743	0.031	0	0	0	0	
Saps	0	0.010	0.930	0	0	0	0	0
Sapl	0	0	0.010	0.958	0	0	0	0
Juv1	0	0	0	0.010	0.981	0		
Juv2	0	0	0	0	0.013	0.988	0	
Adt1	0	0	0	0	0	0.012	0.992	0
Adt2	0	0	0	0	0	0	0.008	0.992

A. mono

	Csdl	Sdl	Saps	Sapl	Juv1	Juv2	Adt1	Adt2
Csdl	0	0	0	0	0	0	1200	4800
Sdl	0.169	0.645	0.037	0	0	0	0	0
Saps	0	0.005	0.911	0.022	0	0	0	0
Sapl	0	0	0.002	0.938	0	0	0	0
Juv1	0	0	0	0.005	0.976	0	0	0
Juv2	0	0	0	0	0.003	0.985	0	0
Adt1	0	0	0	0	0	0.008	0.983	0
Adt2	0	0	0	0	0	0	0.017	0.996

A. rufinerve

	Csdl	Sdl	Saps	Sapl	Madt1	Madt2	Fadt1	Fadt2
Csdl	0	0	0	0	0	0	1200	4900
Sdl	0.185	0.856	0.086	0	0	0	0	0
Saps	0	0.030	0.853	0	0	0	0	0
Sapl	0	0	0.002	0.996	0	0	0	0
Madt1	0	0	0	0.004	0.972	0	0	0
Madt2	0	0	0	0	0.008	0.968	0	0
Fadt1	0	0	0	0	0.020	0	0.700	0
Fadt2	0	0	0	0	0	0.0324	0	0.929

b) In gaps

A. amoenum

	Csdl	Sdl	Saps	Sapl	Juv1	Juv2	Adt1	Adt2
Csdl	0	0	0	0	0	0	140	560
Sdl	0.449	0.735	0.020	0	0	0	0	0
Saps	0	0.010	0.948	0	0	0	0	0
Sapl	0	0	0.009	0.972	0	0	0	0
Juv1	0	0	0	0.014	0.975	0	0	0
Juv2	0	0	0	0	0.025	0.959	0	0
Adt1	0	0	0	0	0	0.041	0.991	0
Adt2	0	0	0	0	0	0	0.009	0.997

A. mono

	Csdl	Sdl	Saps	Sapl	Juv1	Juv2	Adt1	Adt2
Csdl	0	0	0	0	0	0	1200	4800
Sdl	0.567	0.767	0.048	0	0	0	0	0
Saps	0	0.047	0.884	0	0	0	0	0
Sapl	0	0	0.003	0.951	0	0	0	0
Juv1	0	0	0	0.017	0.935	0	0	0
Juv2	0	0	0	0	0.065	0.957	0	0
Adt1	0	0	0	0	0	0.043	0.966	0
Adt2	0	0	0	0	0	0	0.023	0.996

A. rufinerve

	Csdl	Sdl	Saps	Sapl	Madt1	Madt2	Fadt1	Fadt2
Csdl	0	0	0	0	0	0	1200	4900
Sdl	0.315	0.862	0.045	0	0	0	0	0
Saps	0	0.064	0.897	0.0505	0	0	0	0
Sapl	0	0	0.013	0.905	0	0	0	0
Madt1	0	0	0	0.024	0.927	0	0	0
Madt2	0	0	0	0	0.049	0.969	0	0
Fadt1	0	0	0	0	0.0244	0	0.786	0
Fadt2	0	0	0	0	0	0.0309	0.000	0.929

canopy, except for *Ar* at the adult tree stages (DBH 20 - 30 cm, ≥ 30 cm) (Fig. 6, Wilcoxon's two-sample test, $p < 0.05$). While *Ar* showed a higher DBH growth rate than *Am* and *Aa* at the juvenile tree stage (DBH 5 - 10 cm) in gaps, the growth rate of *Aa* was comparable to that of *Ar* at the same stage under closed canopy. A decrease in growth rate with an increase in tree size was apparent for *Aa*, both in gaps and under a closed canopy (Tukey's HSD test, $p < 0.05$), but not for *Am* in gaps or for *Ar* under closed canopy (Tukey's HSD test, $p > 0.5$).

Life-history characteristics in the matrix model

Field observation showed that the minimum size for reproduction was the smallest for *Ar* (DBH 2.4 cm), largest for *Am* (DBH 12.7 cm) and intermediate for *Aa* (DBH 8.0 cm), in correspondence with the rank order of maximum tree size for the species (Shibata & Tanaka 2002). The critical DBH size for reproduction (flowering) estimated from the logistic regression was 3.5 cm for *Ar*, 11.0 cm for *Aa* and 18.2 cm for *Am* (Thomas 1996, Fig. 7). We set the critical size of reproduction in the matrix model analysis operationally at DBH 5 cm, 15 cm and 20 cm for *Ar*, *Aa* and *Am*, respectively, because all of the sampled individuals larger than these sizes were observed to flower at least once during the observation period (Fig. 7, Tanaka unpubl.). Because fecundity was low close to critical tree size for flowering, any error introduced by our conservative estimation of this parameter likely has little influence in calculating population vital rates.

Ar individuals underwent sex change (Matsui 1995, Nanami et al. 2004) from male to female at the rate of ca. 3%/yr (H. Tanaka unpubl.) and had higher mortality than the other species in the female adult stages (Fadt1 & Fadt2) (Table 1).

While transition (progression) probabilities from small (Saps) to large (Sapl) saplings under a closed canopy were very low (0.2%) for *Am* and *Ar*, *Aa* maintained a higher progression probability (1%) even under a

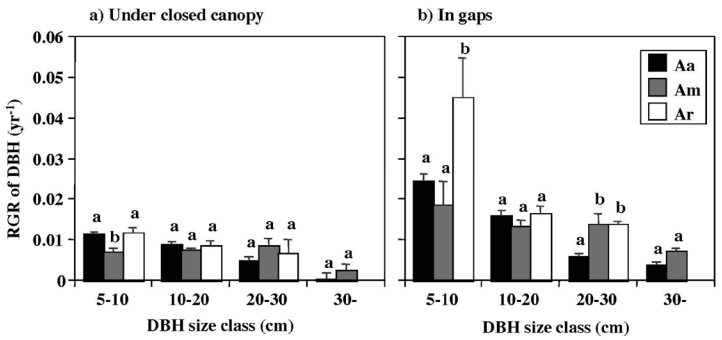

Fig. 6. Relative growth rate of trees with a DBH larger than 5cm (**a**) under closed canopy and (**b**) in gaps. Means + SE. Different letters indicate significant differences between the species within size classes (Tukey's HSD test, $p < 0.05$).

Table 2. The population growth rate (λ) of three maple species calculated from the Shaded, Gap, and Combined population matrix models, and the corresponding 95% boot-strap confidence intervals.

		matrix model		
	statistic	Shaded	Gap	Combined
Aa	λ	1.011	1.028	1.013
	95% CI	1.000-1.019	0.994-1.042	1.000-1.018
Am	λ	0.998	1.071	1.015
	95% CI	0.992-1.002	0.984-1.105	0.992-1.038
Ar	λ	1.015	1.116	1.050
	95% CI	0.987-1.035	0.957-1.187	0.997-1.112

closed canopy (Table 1). For all species, the probabilities for remaining at the same life stage (stasis) were higher than those for progression or for retrogression (moving back to the smaller life stages). Notably, stasis at life stages later than Sapl was > 90% reflecting the high survival rate and slow growth at those stages. In gaps, progression increased and stasis decreased compared to those under closed canopy, reflecting the increase of growth rates in the gaps.

All species exhibited some degree of probability for retrogression at the seedling and sapling stages both in gaps and under a closed canopy (Table 1). These results were caused by death of terminal branches, stem breakage and dieback of a tree's above-ground parts, which was especially notable for *Ar* at the small sapling (Saps) stage (9%). In the smaller size classes (earlier life stages), the probabilities of progression were substantially lower and the mortality was higher than for the larger size classes (later life stages) for all species both under closed canopy and in gaps.

Population growth rate

The population growth rates (λ) of the shaded populations of *Aa* and *Ar* were >1 (1.011 and 1.016, respectively), while that of *Am* was slightly <1 (0.998). However, the estimated 95% CI of all species included 1, suggesting that all species can maintain a stable population, even under closed canopy (Table 2).

On the other hand, gap populations all had λ > 1 (1.028, 1.071, 1.116 for *Aa*, *Am*, *Ar*, respectively, Table 2), suggesting a high potential for population size increase in gaps. The relatively larger variation of the estimated λ for the gap populations of each species can be attributed to the small sample size of the gap populations. The ratio of the increase (λ in gaps / λ under a closed canopy) was highest for *Ar* (1.098) and lowest for *Aa* (1.017).

Under the present canopy disturbance regime (for the combined population), all of the species had a population growth rate ≥1, but only *Aa* had a rate significantly > 1 (Table 2).

Elasticities

The contributions of survival, growth and fecundity at different life stages and canopy conditions to population growth were examined with elasticity analysis, and the relative importance of the demographic parameters was found to be different among the species (Table 3, App. 1). The relative importance of survival (stasis) at juvenile and adult stages under closed canopy was high for *Aa*. While survival at the same life stages under closed canopy were also important for *Am*, it is notable that survival at juvenile and adult stages in gaps were equally important for *Am*. In contrast to *Aa*, relative importance of survival and growth (progression) at the seedling and sapling stages in gaps was high for *Ar*. The high elasticity for adult stage survival was common to the three species (Table 3). Elasticity of fecundity was generally low for all three species, but *Ar* showed relatively high elasticity value for the fecundity compared to the other species.

Projected stable population structures

Projected stable population structures based on the combined population model were different from the present population structures for all the *Acer* species (Fig. 8). The relative frequency of tree stages (juvenile and adult) of the projected stable stage distribution was distinctly lower than the present stage distribution for AR and AM, but higher for AA.

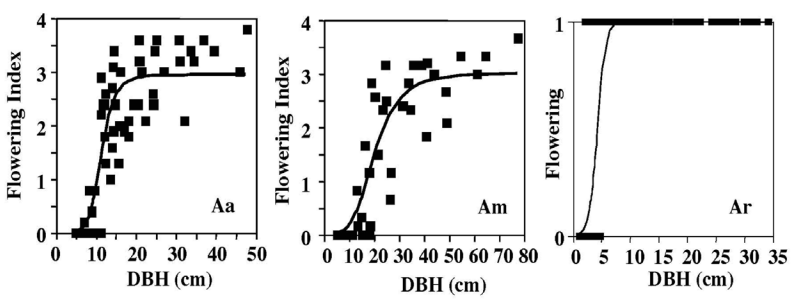

Fig. 7. Critical size of flowering for three *Acer* species.

Table 3. Summary of elasticity of combined matrix model at each life stage for shaded and gap sub-populations. Elasticity values > 10 % are in bold.

sp	Growth stage	Sub-population					
		shaded			gap		
		stasis	progression	fecundity	stasis	progression	fecundity
Aa	Csdl	0.0%	0.5%	-	0.0%	0.1%	-
	Sdl	1.3%	0.5%	-	0.2%	0.1%	-
	Saps	5.6%	0.5%	-	0.8%	0.1%	-
	Sapl	8.7%	0.5%	-	1.1%	0.1%	-
	Jev1	**15.2%**	0.5%	-	1.5%	0.1%	-
	Jev2	**18.2%**	0.4%	-	1.5%	0.1%	-
	Adt1	**23.0%**	0.3%	0.2%	2.4%	0.0%	0.0%
	Atl2	**14.9%**	0.0%	0.3%	1.5%	0.0%	0.0%
Am	Csdl	0.0%	0.1%	-	0.0%	1.0%	-
	Sdl	0.1%	0.0%	-	2.6%	1.1%	-
	Saps	1.1%	0.1%	-	4.9%	1.0%	-
	Sapl	2.1%	0.1%	-	7.5%	1.0%	-
	Jev1	4.2%	0.1%	-	6.9%	1.0%	-
	Jev2	8.1%	0.2%	-	8.4%	0.9%	-
	Adt1	**11.5%**	0.3%	0.0%	8.4%	0.4%	0.4%
	Atl2	**17.3%**	0.0%	0.1%	8.4%	0.0%	0.6%
Ar	Csdl	0.0%	0.2%	-	0.0%	2.4%	-
	Sdl	1.4%	0.2%	-	8.5%	2.6%	-
	Saps	1.1%	0.1%	-	**10.6%**	2.5%	-
	Sapl	5.1%	0.2%	-	**10.8%**	2.5%	-
	Madt1	3.7%	0.1%	-	**12.6%**	1.9%	-
	Madt2	4.3%	0.0%	-	**13.7%**	0.0%	-
	Fadt1	0.1%	0.0%	0.0%	1.4%	0.0%	0.6%
	Fadt2	2.6%	0.0%	0.2%	8.6%	0.0%	1.8%

Discussion

Although the size class distribution of trees with DBH > 5 cm suggested that *Ar* is a light demanding, gap-dependent species (bell-shaped curve) and that the other two species (*Aa* and *Am*) are shade-tolerant (L-shaped curve) (Masaki et al. 1992), a high survival rate of seedlings and saplings under a closed canopy in comparison with the other major tree species in this forest community (Shibata & Nakashizuka 1995; Abe et al. 1998; Masaki & Nakashizuka 2002) indicated that the three *Acer* species are all conventional shade-tolerant species (Shugart 1984). Population growth rates (λ) ≈ 1 of the shaded populations of all three species also suggested a high potential for maintaining populations under a closed canopy. Furthermore, there was no indication

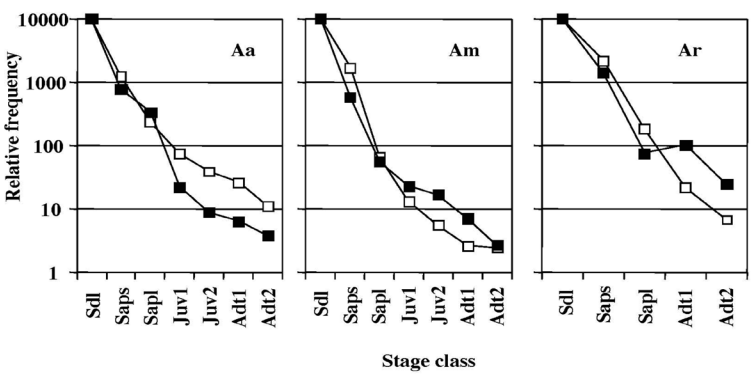

Fig. 8. Present distribution of life stages (black square) and projected stable stage distribution (white square) of three *Acer* species.

of a clear trade-off between survival under a closed canopy and growth in a gap (Kobe et al. 1995; Pacala et al. 1996) among either the seedlings or saplings. Notably, *Ar* showed both adaptation to the gap environment (high potential growth rate) and a high shade tolerance (survival).

Nor was there a clear trade-off between growth under closed canopy and in the gaps (Thomas & Bazzaz 1999). The ranking of the three species by growth rate was generally consistent under closed canopy and in the gaps. However, a change in their relative positions along the spectrum of growth rate under closed canopy was detected as the plants increased in size from seedling to sapling. Between the small sapling stage and the large sapling stage, a cross-over in the light requirement (as defined by Grubb 1996) occurred among the species (Fig. 5a). Only at the small sapling stage was a trade-off between growth under closed canopy and in the gaps apparent, and *Aa* had an advantage over the other two species under closed canopy, compensating for its disadvantage in gaps.

High survival of the three *Acer* species at the seedling and sapling stages under closed canopy may be determined by both physiological and architectural (or morphological) characteristics (Kitajima 1994; Sipe & Bazzaz 1994; Sack & Grubb 2001; Dalling et al. 2001). Intraspecific differences in leaf features under shady conditions are relatively small in these species (Hanba et al. 2002). Negative mean growth rate and high survival rate of *Ar* at the small sapling stage under closed canopy may be explained by the species' ability to survive after death or breakage of a terminal shoot or main stem. Damaged or suppressed seedlings and saplings under closed canopy survive by being unbranched, possessing only one pair of relatively large leaves and by creeping on the forest floor (often producing adventitious roots, H. Tanaka, pers. obs.). This habit seems to be similar to that of *A. pensylvanicum*, which is a subcanopy species of eastern North America and is phylogenetically close to *Ar* (Sipe & Bazzaz 1994). The production of adventitious roots occurs for all three species here, but is most prominent in AR.

The life-history differences in these three non-pioneer *Acer* species were demonstrated by matrix analyses both in population growth rate (λ) and elasticity values. Relative importance of gaps for population maintenance (indicated in the λ value) was highest for *Ar*, medium for *Am* and lowest for *Aa* (Table 2). According to the elasticity analyses, the importance of survival at later life stages (juvenile and adult tree stages) under closed canopy was clear for *Aa*, corresponding to the shade-adapted characteristics of this long-lived sub-canopy tree (Table 3). For *Am*, the importance of survival at the juvenile and adult tree stages was found not only under closed canopy, but also in gaps, corresponding to the shade-tolerant, but canopy-adapted characteristics of this species (Table 3). The importance of survival at the seedling and sapling stages as well as in the adult stage (especially in gaps) was clear for *Ar*, corresponding to its shade-tolerant, but gap-adapted characteristics as a short-lived, gap-phase (*sensu* Barnes et al. 1998) sub-canopy tree (Table 3). Overall, the high growth rate of *Ar* in stages later than the large sapling both in gaps and under a closed canopy, lower critical size of reproduction and high mortality at the female adult stage, all contributed to the high turnover rate (or low longevity) and the small maximum DBH of the species. Other adjustments, such as trade-offs between maximum DBH and recruitment rate (Kohyama 1993) or between longevity and growth rate (Crawley 1997), may occur in these species and are relevant for the coexistence in a forest community (Silvertown 2004).

The stable stage distribution projected by the combined matrix model assuming that the present disturbance regime will continue, showed certain differences from the present distribution for all the species. Relative frequencies of the stages later than the sapling stage of the stable stage distributions were lower than those of the present stage distributions for *Ar* and *Am*, but higher for *Aa* (Fig. 8). This suggests that the present population structures of the three species are not in equilibrium. These discrepancies between observed and projected stable stage distribution may be partly explained by the occurrence of large-scale anthropogenic disturbances in the last century (Suzuki 2002). Large-scale disturbances may have strongly facilitated recruitment from the sapling to the juvenile stage for gap-phase *Ar*, moderately facilitated this transition for *Am*, but inversely affected the rate in shade-adapted *Aa*. Further analyses incorporating a variable canopy disturbance regime may help us assess the discrepancies between the realized and projected stage distributions.

Variation or shifts in the light requirements for establishment, growth, survival and reproduction among the different stages through a tree's life history may occur more commonly than we have assumed. Even for the three closely related *Acer* species, such variations were detected at the sapling stage (Fig. 4). To understand the syndrome of traits associated with these shifts, and to be able to classify functional species groups accordingly, we need to gather as much life-history information about various species as possible (Clark & Clark 1992; Dalling et al. 2001; Wright et al. 2003; Silvertown 2004). It is important to clarify quantitatively the size (life-stage) dependent patterns of these traits (gap dependence, shade tolerance) for the component species making up a forest community in order to understand mechanisms responsible for coexistence of species.

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